

Optimization, Conflict, and Nonoverlapping Foraging Ranges in Ants

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ABSTRACT: An organism's foraging range depends on the behavior of neighbors, the dynamics of resources, and the availability of information. We use a well-studied population of the red harvester ant *Pogonomyrmex barbatus* to develop and independently parameterize models that include these three factors. The models solve for an allocation of foraging ants in the area around the nest in response to other colonies. We compare formulations that optimize at the colony or individual level and those that do or do not include costs of conflict. Model predictions were compared with data collected on ant time budgets and ant density. The strategy that optimizes at the colony level but neglects costs of conflict predicts unrealistic levels of overlap. In contrast, the strategy that optimizes at the individual level predicts realistic foraging ranges with or without inclusion of conflict costs. Both the individual model and the colony model that includes conflict costs show good quantitative agreement with data. Thus, an optimal foraging response to a combination of exploitation and interference competition can largely explain how individual foraging behavior creates the foraging range of a colony. Deviations between model predictions and data indicate that colonies might allocate a larger than optimal number of foragers to areas near boundaries between foraging ranges.

Keywords: foraging ranges, competition for space, game theory, optimization models, territoriality.

How can we explain the ways that organisms partition space? In the most visible cases, boundaries between territories are actively defended. Individuals may instead defend resources or attack intruders within a foraging range

(Hölldobler and Lumsden 1980). Even without active defense, organisms may partition space into nonoverlapping foraging ranges to avoid exploitation competition. Exploitation competition can deter intruders if an individual can systematically exploit resources in its foraging range, thus reducing the mean availability of resources and removing attractive high-density patches (Davies and Houston 1981; Possingham 1989). Overexploitation of resources near the boundary could also act as a deterrent to intruders (Paton and Carpenter 1984; Lucas and Waser 1989).

Space partitioning is determined by the ways that individuals allocate effort within a territory or foraging range. Understanding how these individual decisions lead to partitioning of space in particular cases has proven difficult. As Adams (2001) points out in a recent review, few theoretical models of space partitioning have combined the many realities that challenge organisms: distance (Harkness and Maroudas 1985; Holder Bailey and Polis 1987), familiarity and information (Stamps and Krishnan 2001), resource distribution (Crist and Haefner 1994), and risks from conflict with neighbors and predators (Hamilton 1971).

In group foraging species, as in individually foraging ones, individual behaviors create emergent patterns. Rather than considering how space is partitioned among groups, this literature has concentrated on how group size and composition is determined by the costs and benefits of different behaviors (Hake and Ekman 1988; Livoreil and Giraldeau 1997). Foragers must address a set of conflicting demands similar to those faced by individual foragers, including trade-offs between foraging success and predation risk (Hamilton 1971; Poysa 1987), the use of information (Smith et al. 2001; Templeton and Giraldeau 1995), and the quality of information (Valone 1993) and spatial effects (Ruxton 1995).

Models of territorial behavior or group foraging can seek to explain spatial patterns by finding which individual behaviors are consistent with patterns observed at the colony and population scales or by deriving individual behaviors using optimal foraging theory. Understanding how

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optimal foraging behavior, within informational and cognitive constraints, leads to space use requires developing spatially explicit models that make testable predictions at both the individual and population level. Previous studies have addressed organisms ranging from birds (Hake and Ekman 1988) and bees (Dukas and Edelman-Keshet 1998) to wolves (Lewis and Murray 1993) and trees (Lopez et al. 1994).

We use a well-studied population of the red harvester ant *Pogonomyrmex barbatus* (Gordon 1999) to build and parameterize models that include the behavior of neighbors, resource dynamics, and a simple model of information sharing. The models find foraging ranges as the solution of a game that takes into account the responses of neighbors, and the models predict the location of boundaries between the foraging ranges of neighboring colonies, the degree of overlap, and the spatial distribution of foragers. We test our models with observations of individual ants and counts of density.

Whether through defense, avoidance, or exploitation competition, low overlap in foraging ranges is characteristic of harvester ants. Active defense and avoidance have been observed in these ants (Harrison and Gentry 1981; Acosta et al. 1995; Gordon and Kulig 1996), as has the deterrent effect of exploitation competition (Dreisig 2000). The breadth of previous work on the individual behaviors that create patterns of foraging range overlap makes these ants an ideal system to build models that elucidate mechanisms. Studies of seed-harvesting ants in several genera have addressed time and energy budgets (MacKay 1985; Fewell 1988; Weier and Feener 1995), foraging behavior (Davidson 1977; Fewell 1990; Crist and MacMahon 1991, 1992; Crist and Haefner 1994; Ferster and Traniello 1995; Morehead and Feener 1998; Gordon 2002), and colony interactions (Davidson 1977; DeVita 1979; Harrison and Gentry 1981; Gordon 1992; Ryti and Case 1992; Lopez et al. 1994; Wiernasz and Cole 1995; Yamaguchi 1995; Gordon and Kulig 1996; Dreisig 2000).

Our models build on a well-developed modeling framework that has been used to describe the foraging ranges of individual organisms as well as colonies. Early models of foraging range derive optimal territory area in response to resources and intruders (Schoener 1987). These models are spatially implicit in solving only for area. Because they treat other foragers as a spatially distributed intruder pressure, they do not treat competition with neighbors explicitly.

Later models use the analogy to pressure to model the spatial distribution of multiple abutting territories (Brisson and Reynolds 1994; Korzukhin and Porter 1994; Adams 1998). Territorial boundaries are assumed to lie at points where the pressures from neighboring colonies are equal (Adams 1998). Using an expression for pressure that de-

pends on the size of the colony, the foraging area, and the distance from the nest, Adams's (1998) model accurately predicts areas and shapes of territories. However, models of this type make no predictions about the behavior or locations of individuals (or roots in the case of plants), assume that foraging ranges do not overlap, and are not based on an explicit cost-benefit analysis.

Lewis and Murray (1993) and Lewis et al. (1997) developed a model of display behavior that predicts the shape, size, and degree of overlap between wolf territories. Their model derives the locations of boundaries and the degree of overlap but, like pressure models, assumes movement rules and has no measures of the costs and benefits of different strategies.

A first step in building spatially explicit models of optimizing competitors was Maynard Smith's (1982) one-dimensional game theoretic model, where each individual chooses a display strategy that depends on the distance from the center of its foraging range. This model emphasized costs of conflict but includes only phenomenological benefits of territory size and is restricted to two competitors in a one-dimensional habitat. Lewis and Moorcroft (2001) use their spatially explicit model of wolves and deer (Lewis and Murray 1993; Lewis et al. 1997) to parameterize a one-dimensional model of the game between two neighboring wolf packs and find an evolutionarily stable level of avoidance of scent marks.

The models presented in this article derive from a slightly different theory lineage (Getty 1981; Tullock 1983). Models of this type assign a value to each location in space as a function of distance to the central place for that forager and a measure of exploitation or interference competition from other foragers. From these values, the optimal allocation of effort in space can be computed when multiple individuals or colonies compete. However, in the original models (Getty 1981; Tullock 1983), costs of distance and competition are not derived from underlying resource dynamics or the quantitative effects of encounters with neighbors.

Our approach is most similar to a model of wagtails (Davies and Houston 1981). Using a fully parameterized description of the resource dynamics, feeding rates, and the costs of defense characteristic of wagtails, Davies and Houston (1981) predict whether a territory owner should accept a "satellite" that aids in defense at the cost of depleting resources. This model assigns a value to locations on the basis of a mechanistic accounting of time and energy budgets and makes accurate predictions of behavior on the basis of optimization principles.

The model of wagtails is simpler than our extension to ant colonies because these birds can systematically search their territories to minimize inefficiency, leading to a simple pattern of effort allocation in space. As members of a

colony that operates without central control in a complex two-dimensional environment (Gordon 1999), ants cannot systematically search their foraging range. Instead, individual ants must choose a foraging strategy on the basis of information received from other ants (Adler and Gordon 1992; Gordon 2002). We model information limitation in two complementary ways. First, we build models with and without the assumption that ants know the foraging ranges of neighboring colonies and can assess the expected costs of conflict. Ignorance of the detailed locations of neighbors is plausible given the rarity of encounters between ants of different colonies (Gordon and Kulig 1996). Second, we compare ants that maximize the seed collection rate at the individual level with those that use information about the whole colony to maximize at the colony level. The former strategy is suboptimal but simple to achieve by equalizing seed collection rate across foragers (Bartholdi et al. 1993; Pacala et al. 1996; Dukas and Edelman-Keshet 1998).

After deriving the contrasting models that optimize at the colony or individual level, we use measurements from earlier studies of this population to fully parameterize the models and predict time budgets of foragers and patterns of foraging range overlap. We compare these predictions with data collected for this study, evaluate which model fits the data most closely, and explore possible reasons for deviations.

The Models

A colony of ants must allocate foraging effort throughout space in response to resource availability, travel time, and conflict with other ants (Harkness and Maroudas 1985; Haefner and Crist 1994; Dukas and Edelman-Keshet 1998). What currency might we expect ants to optimize? Several studies have shown that energy costs of travel are low in harvester ants (Fewell 1988; Weier and Feener 1995), implying that rate maximization coincides with efficiency maximization. Furthermore, studies of a related species have shown that ants maximize energy intake divided by time rather than efficiency (Holder Bailey and Polis 1987).

Harvester ants collect seeds that are heterogeneous in size and spatial distribution. For simplicity, our models treat all seeds as equivalent because earlier studies indicate that *Pogonomyrmex barbatus* does not choose seeds on the basis of size (Morehead and Feener 1998). We simplify by treating the distribution of resources as homogeneous for two reasons. First, a study of seeds collected by foragers in this population (Gordon 1993) showed no relation between the vegetation currently growing in the foraging area and the species of seeds collected by the ants; most seeds are apparently distributed by wind and flooding. This

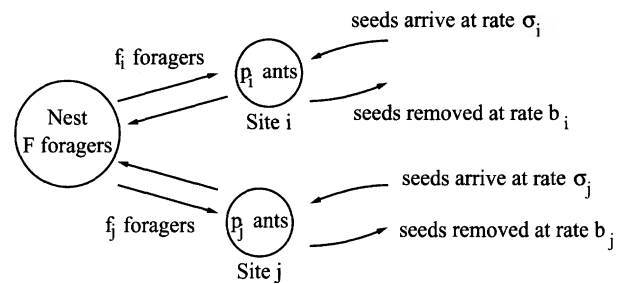


Figure 1: Structure of the allocation decision and seed dynamics model. The colony assigns f_i out of F foragers to site i , of which p_i are searching for seeds.

study showed that the seed distribution is patchy on the scale of distances between nests rather than the smaller scale of different foraging trails. Second, the seed distribution is ephemeral, with patches persisting only for some weeks. Because our models are designed to predict average space use over an entire season, we assume that the quality of different locations averages out over time.

In this simplified resource environment, available information constrains the strategy that maximizes the rate of seed collection. We examine two possible strategies that ants could use to allocate foragers in space. In the first, which we call the colony-level model, ants find the allocation that maximizes the rate of seed collection by the colony. Achieving optimal allocation requires individual ants to assess the foraging strategy of the entire colony or correct for local density of ants (Pacala et al. 1996). In the second, which we term the individual-level model, each ant seeks the site that provides it with the highest individual rate of intake. This leads to the equalization of intake rates among foragers (Pacala et al. 1996; Dukas and Edelman-Keshet 1998) and is simple because ants need not assess any information about the entire colony. We begin by deriving and comparing the two strategies for a single colony and then extend the models to address multiple colonies in competition.

The Single Colony Model

For a single colony, our models are similar to those presented by Dukas and Edelman-Keshet (1998). Consider a colony with F foragers to be allocated among n sites (fig. 1). Resources in site i are renewed at rate σ_i (tables 1 and 2 have complete descriptions of variables and parameters). Let p_i represent the number of foragers searching for resources in site i . Suppose that resources are removed by other agents that have an effect equivalent to b_i ants. The total resource collection rate from site i , W_i , is then

Table 1: Variables

Symbol	Meaning
i	Index for sites
n	Number of sites
f_i	Number of foragers assigned to site i
p_i	Number of foragers searching in site i
R_i	Number of seeds in site i
W_i	Rate of seed collection in site i
d_i	Distance to site i
τ_i	Travel time to site i

$$W_i = \sigma_i \frac{p_i}{b_i + p_i}. \tag{1}$$

The total resource collected, W , is the sum over all sites, or

$$W = \sum_{i=1}^n W_i. \tag{2}$$

The number of foragers allocated to site i is f_i , with the constraint

$$F = \sum_{i=1}^n f_i, \tag{3}$$

where F is the total number of foragers available. Because foragers spend time traveling, the number allocated, f_i , is greater than the number searching, p_i . To derive the relationship between f_i and p_i , we need to compute the time spent searching and traveling by each ant.

A forager switches back and forth between travel and searching. The fraction of time spent searching is the rate of switching from travel to search divided by the sum of both switching rates (Adler 1998). Travel time to site i is τ_i , equal to the travel distance d_i divided by the speed v . We approximate the rate of switching from traveling to searching as the reciprocal, or $1/\tau_i$.

To find the switching rate from searching to travel, we use our model of seed dynamics. Suppose that the number of seeds R_i in site i follows the differential equation

$$\frac{dR_i}{dt} = \sigma_i - \eta(b_i + p_i)R_i,$$

where η is the per seed rate at which a forager collects resources. If the resources are in quasi steady state, they remain near the equilibrium of $R_i = \sigma_i/[\eta(b_i + p_i)]$. The rate at which resources are found, and, thus, the rate at which an ant switches from searching to travel, is ηR_i . The fraction of foragers that are searching for food is then

$$\frac{p_i}{f_i} = \frac{1/\tau_i}{(1/\tau_i) + [\sigma_i/(b_i + p_i)]}.$$

Solving for f_i gives

$$f_i = \left(1 + \frac{\sigma_i \tau_i}{b_i + p_i}\right) p_i. \tag{4}$$

The parameter η does not appear in this equation and need not be estimated.

Using these relationships, we can find the colony-level strategy (that maximizes the colony-wide seed collection rate) and the individual-level strategy (that maximizes individual rates). The colony-level strategy is found with Lagrange multipliers (Kaplan 1984), maximizing W subject to the constraint on F and the requirement that $p_i > 0$. Because both W and F are sums, the maximum occurs where marginal rates of return are equal (Pacala et al. 1996), or

$$\frac{\partial W_i}{\partial f_i} = \mu_c.$$

We can then solve for p_i as

Table 2: Parameters

Symbol	Meaning	Estimate
σ	Resource renewal rate	.1 seed/min
F	Number of foragers	1,890 (adult colony)
v	Speed	2.5 m/min
b	Foraging pressure from other agents	1.0/m ²
α	Rate at which quarrels begin	.01/(min ant ² m ²)
β	Rate at which quarrels end	1.5/min
s	Probability a quarrel escalates	.07
γ	Rate at which fights end	.025/min
δ	Probability a fighting ant is killed	.7
M	Value of a lost forager	50 seeds

$$p_i = \sqrt{\sigma_i b_i \left(\frac{1}{\mu_c} - \tau_i \right)} - b_i. \quad (5)$$

The individual-level strategy is found by setting the returns per ant equal, or

$$\frac{W_i}{f_i} = \mu_e.$$

This equation can be solved for p_i as

$$p_i = \sigma_i \left(\frac{1}{\mu_e} - \tau_i \right) - b_i. \quad (6)$$

for some value of μ_e that need not equal μ_c .

To solve for either the colony-level or individual-level strategy, we constrain p_i to be positive in equation (5) or equation (6) and sum the associated values of f_i from equation (4). This gives an equation for μ_c or μ_e in terms of the available foragers F that can be solved numerically.

The two strategies show characteristic differences that appear again in the multiple colony models. If ants follow the colony-level strategy, the colony collects more resources by allocating more ants to greater distances (fig. 2a) and having those ants collect less resource per unit time (fig. 2b). If ants follow the individual-level strategy, the colony overexploits sites near the nest but receives only a slightly lower payoff in seeds per minute over a wide range of forager numbers (fig. 2c). Although the individual-level strategy is not optimal, it uses no global information, is robust in changing environments, and reduces colony intake rate only slightly (Bartholdi et al. 1993; Pacala et al. 1996; Seeley 1997).

Multiple Colony Models

The model extends immediately to include exploitation competition between colonies by including the resources removed by other colonies in the term b_i . In particular, for each colony, let \tilde{p}_i represent the number of ants from other colonies foraging in site i . The solutions found in equations (5) and (6) give the best reply to any given strategy by competing colonies if we substitute $b_i + \tilde{p}_i$ for b_i . We can find a Nash equilibrium (a best reply to a best reply) for this model of exploitation competition with iteration.

Interference competition creates two additional costs: time and mortality (fig. 3). Fighting reduces the fraction of time spent searching (Gordon and Kulig 1996). To account for fighting time, we break fighting pairs into two categories (Gordon and Kulig 1996): brief quarrels that

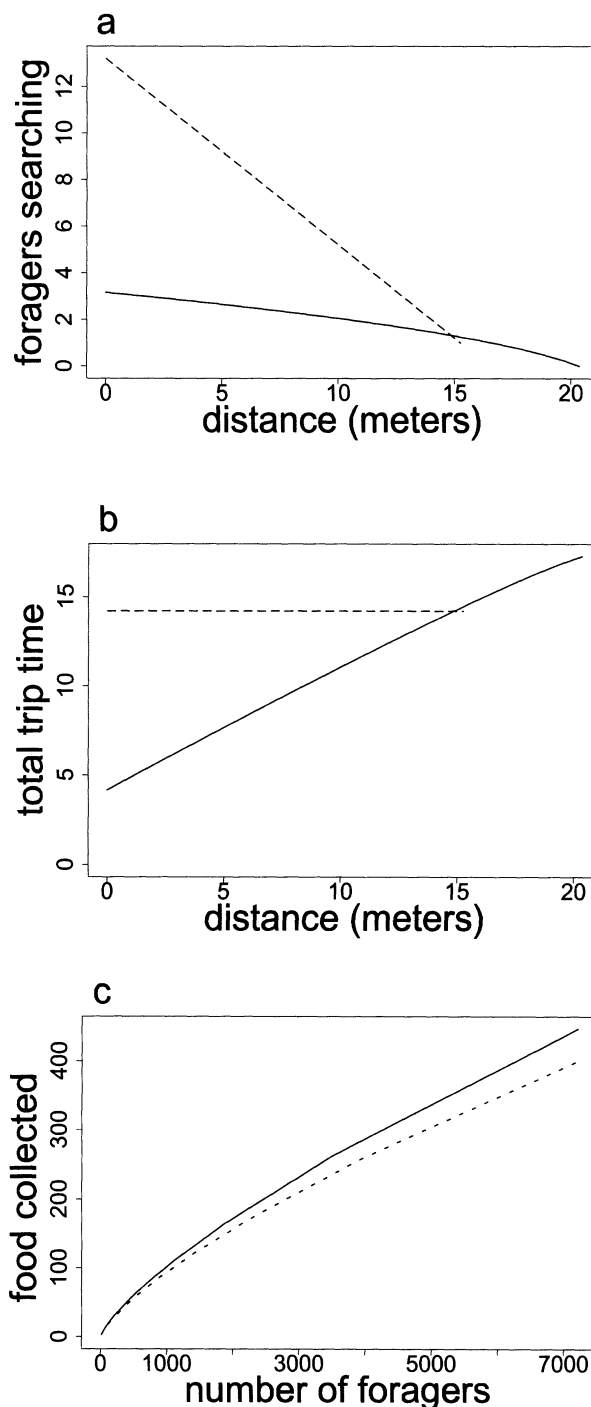


Figure 2: Single colony results. We compare the colony-level strategy (solid lines) with the individual-level strategy (dashed lines) using relevant parameter values from table 2. a, Number of foragers allocated per square meter as a function of distance from the nest. b, Total trip time as a function of distance from the nest. c, Seeds collected per minute as a function of number of foragers.

do not lead to injury (q_i) and escalated fights (\bar{q}_i). If a focal colony with p_i foragers encounters other colonies with \tilde{p}_i foragers, these pairs follow the differential equations

$$\begin{aligned}\frac{dq_i}{dt} &= \alpha p_i \tilde{p}_i - \beta q_i \\ \frac{d\bar{q}_i}{dt} &= \beta s q_i - \gamma \bar{q}_i,\end{aligned}$$

where α is the rate at which quarrels begin per pair of ants in a square meter, β is the rate at which quarrels end, s is the probability of escalation, and γ is the rate at which fights end (table 2). If quarrels and fights are in quasi steady state, $q_i = (\alpha/\beta)p_i \tilde{p}_i$ and $\bar{q}_i = (\alpha s/\gamma)p_i \tilde{p}_i$. The total number of foragers allocated to the site (f_i) is the sum of those foraging (p_i), those traveling (m_i), those quarreling (q_i), and those fighting (\bar{q}_i). If we set $A = \alpha[(1/\beta) + (s/\gamma)]$, the average time spent quarreling or fighting per foreign ant, then

$$f_i = \left(1 + \frac{\sigma_i \tau_i}{b_i + p_i + \tilde{p}_i} + A \tilde{p}_i\right) p_i. \quad (7)$$

This extends equation (4) to include a new term for ants engaged in fights.

If fighting also incurs mortality or severe injury with probability δ (Gordon and Kulig 1996), the normalized rate of forager loss can be subtracted from the intake rate. Let M represent the value of an ant in units of seeds, and let $K = \alpha s \delta M$ be the rate at which such value is lost as a result of fights per ant pair per square meter. Then, the net intake W_i in site i is

$$W_i = \sigma_i \frac{p_i}{b_i + p_i} - K p_i \tilde{p}_i.$$

The model with no interference competition can be studied by setting $\alpha = 0$.

Colony-level and individual-level strategies are found as in the single colony case, but the solutions include additional terms. With the colony-level strategy,

$$p_i = \sqrt{\frac{\sigma_i(b_i + \tilde{p}_i)[(1/\mu_c) - \tau_i]}{1 + [\alpha + (K/\mu_c)]\tilde{p}_i}} - (b_i + \tilde{p}_i).$$

With the individual-level strategy,

$$p_i = \frac{\sigma_i[(1/\mu_c) - \tau_i]}{1 + [\alpha + (K/\mu_c)]\tilde{p}_i} - (b_i + \tilde{p}_i).$$

As before, we solve each equation for the values of μ_c and μ_e that give a total forager number of F when p_i is constrained to be positive. Solutions are iterated because the value \tilde{p}_i depends on the strategy of other colonies.

In particular, we start each colony with the single colony optimum, find the best reply for each colony to that set of strategies, and repeat until the strategies stop changing. To improve convergence, we do not entirely replace the old strategy with its best reply but instead with a weighted average of the original strategy (weighting 0.8) and the best reply (weighting 0.2). Failure to include this weighting can lead to an oscillation between strategies rather than convergence, which is an artifact of assuming that each colony responds instantaneously to the fixed strategies of the others. Including the weighting better approximates a system where colonies respond gradually and simultaneously.

Parameter Estimation

All model runs use ant parameters estimated independently in an earlier study (Gordon and Kulig 1996) and seed parameters estimated at other desert sites. We break parameters into three general categories: those describing seed dynamics, those describing foraging behavior of a single colony, and those describing encounters between ants from different colonies.

Seed Dynamic Parameters

These parameters describe seed dynamics in the absence of red harvester ants. We estimate the resource renewal rate, σ , as 0.1 seed/min (which corresponds to about 50,000 seeds/yr). This value is consistent with that observed in other North American deserts (Price and Reichman 1987; Kemp 1989) but assumes a somewhat shorter residence time of seeds than estimated in those studies (about 1 mo instead of 5 mo) because our models focus on the summer foraging season. If we assume a seed residence time of 5 mo, a lower value of $\sigma = 0.05$ seed/min is required to match the observed standing crop of 7,000 seeds/m² (Price and Reichman 1987; Kemp 1989). The seeds studied in these works are collected by red harvester ants (Gordon 1993).

We estimate the rate b at which seeds are removed by causes other than *Pogonomyrmex barbatus* as 1.0 ant equivalent per square meter. This is a small value relative to the number of ants at this location (a mean of roughly five ants per square meter) for several reasons. First, there are few ant competitors for seeds at the site, with unpublished data showing that the density of *P. barbatus* at the site is consistently high relative to that of the other large seed-eating ant, *Aphaenogaster cockerelli*. Other seed-eating spe-

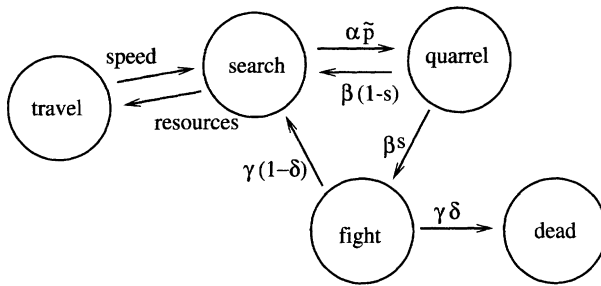


Figure 3: Time budget for an ant. A foraging ant can be engaged in one of four activities: traveling, searching, quarreling (a brief nonescalated encounter with an ant from another colony), and fighting (a longer escalated encounter with an ant from another colony).

cies such as *Pheidole militicida* are smaller and take smaller seeds. Second, populations of seed-eating rodents such as kangaroo rats have sharply declined over the past 10–15 yr in this area. Third, local *P. barbatus* density affects the numbers of reproductives in dry years (Gordon and Wagner 1997) and the survival of founding colonies (Gordon and Kulig 1996), suggesting that depletion by *P. barbatus* is not swamped by other species.

This value of b produces reasonable residence times for seeds and search times for ants. With the resource renewal rate of $\sigma = 0.5$, corresponding to longer seed residence times, a value of $b = 0.3$ ant equivalents per square meter is required to produce realistic search times. Results with these alternative seed parameters are similar to those presented here.

Because the model runs only when ants are actively foraging, and because *P. barbatus* forages for approximately 20% of the day during the foraging season (Gordon 1999), the effective values of b and σ are five times larger.

Ant Foraging Behavior

These parameters describe properties of a single colony. We estimate the number of foragers active in an adult colony, F , as 1,890, which is half of the total number of foragers presented in Gordon and Kulig's (1996) table 5. Only a fraction of foragers actively forage at any one time (Gordon 1999), and we use the value of one-half for simplicity. Some of the model runs include younger colonies, and we again use half the number estimated by Gordon and Kulig (1996): 430 for 1-yr-old, 1,000 for 2-yr-old, 2,000 for 3-yr-old, and 2,600 for 4-yr-old colonies.

We estimate the speed, v , as 2.5 m/min, the average value found by Gordon and Kulig (1996; at the peak of foraging); this matches results found in the measurements made for this article. There is a strong effect of time of day on forager speed, presumably because of temperature

(ranging from as low as 0.8 m/min up to 4.0 m/min). We used the average value because our models make predictions averaged over the entire season.

Ant Fighting Behavior

These parameters describe the rate and severity of encounters between ants. Recall that a quarrel is a brief interaction that does not lead to injury and a fight is an extended interaction that has a high probability of leading to injury or death (fig. 3).

We estimate the rate at which quarrels begin, α , as 0.01/ (min ant² m²). Of 58 foraging trips made in the direction of another colony, 16 ants encountered an ant from another colony (Gordon and Kulig 1996). If we assume that ants spend 75% of foraging time searching, or 15 min, this is a total of 928 ant minutes. If all of this time is spent in areas with a density of three foreign ants/m² (the average density throughout the site found in this study, comparable to the value of five found earlier; Gordon 1995), then the encounter rate is

$$\begin{aligned} \alpha &= \frac{16 \text{ encounters}}{(928 \text{ ant minutes})(3 \text{ ants/m}^2)} \\ &= \frac{0.0057 \text{ encounters}}{\text{min ant}^2 \text{ m}^2}. \end{aligned}$$

We rounded up to 0.01 because these ants did not spend the entire 15-min search period in a region of overlap.

The rate at which quarrels end, β , is about 1.5/min, on the basis of the mean duration of quarrels of 40 s as found by Gordon and Kulig (1996).

We estimate the probability that a quarrel escalates, s , as 0.07. This value is based on the seven fights out of 105 quarrels observed from beginning to end by Gordon and Kulig (1996), or 0.067. Alternatively, of the 28 quarrels not observed from the beginning, 21 out of 28 were fights (Gordon and Kulig 1996). Because fights are approximately 60 times longer than quarrels (and, thus, are 60 times more likely to be detected), the fraction of ants observed to be involved in fights would be

$$\frac{60s}{60s + 1 - s} = \frac{21}{28}.$$

Solving for s gives a separate estimate of 0.047 quarrels that escalate to fights.

The rate at which fights end, γ , is about 0.025/min, on the basis of the mean duration of quarrels of 42 min as found by Gordon and Kulig (1996).

We estimate the probability a fighting ant is injured, δ , at 0.7. Gordon and Kulig (1996) observed 28 fights, in

which 10 ended in death for both ants (we ignore the rare fights involving more than two ants) and 18 in injury or death for one ant. Thus, out of 56 ants involved in fights, 38 were killed or injured. We assume that injured ants no longer forage.

The value of a lost forager, M , we estimate at 50 seeds. Ants live approximately 1 yr (Gordon and Hölldobler 1987). If about 2,000 ants forage and take about 20 min each to collect a seed, then the colony collects 100 seeds/min while foraging. The colony is active for about 10% of the year, or 50,000 min, so the colony collects approximately 5×10^6 seeds/yr. Dividing by the roughly 10,000 ants per colony gives 500 seeds per ant. A forager can expect to live roughly 1 mo (Gordon and Hölldobler 1987), or one-twelfth of its lifespan. Multiplying 500 seeds by this fraction gives 42 seeds.

Combined Parameters

Only two combined parameters that summarize costs of conflict are required to compute the colony-level and individual-level strategies. Mortality costs appear in the model in the single parameter $K = \alpha s \delta M \approx 0.02$ seeds/(min ant² m²). Model runs indicate that even much smaller values of K would be sufficient to deter ants from searching in the foraging ranges of neighboring colonies.

The parameter $A = \alpha[(1/\beta) + (s/\gamma)] = 0.03/(\text{ant}^2 \text{ m}^2)$ represents time costs of encounters. The time wasted in encounters does not play a large role in the avoidance predicted by our models.

Model and Empirical Results

We solved the model using the estimated parameters and true colony locations from the study site near Rodeo, New Mexico (Gordon 1999). We focused on two regions from this site. The crowded region has 12 colonies in a 60×60 -m square, and the uncrowded region has 16 colonies in a 90×90 -m square (fig. 4). The model was solved for the number of ants assigned from each colony to each 1.0-m² site, with foraging ranges of the colonies on the edges allowed to wrap around to avoid edge effects.

In the absence of conflict costs, a population of colonies following the individual-level strategy segregates into separate foraging areas (fig. 5a), while colonies following the colony-level strategy overlap extensively (fig. 5b). A low degree of overlap with the colony-level strategy is predicted only when conflict costs are included (fig. 5c). Although both the colony-level strategy that includes conflict costs and the individual-level strategy predict a realistically low degree of overlap (Gordon and Kulig 1996), the use of space differs. With the individual-level strategy, the density of ants drops off rapidly with distance from the nest and

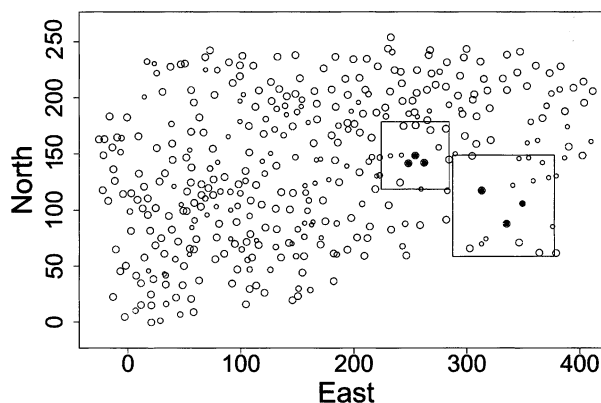


Figure 4: Map of the study area. The open circles represent individual colonies active in 1999. Large circles are adult colonies (>5 yr old), medium circles are adolescent colonies (3–5 yr old), and small circles are juvenile colonies (<2 yr old). The six filled circles show the focal colonies for data collection. The two squares surround the crowded region (*small square*) and uncrowded region (*large square*) followed in the models.

leaves substantial empty space between colonies (fig. 5a). With the colony-level strategy, the density of ants drops off slowly within the foraging range and rapidly at boundaries and leaves no empty space between colonies (fig. 5c).

These differences translate into the distinct predictions about the time budgets of foragers and the spatial distribution of ants that we tested in the field. We made two different types of measurement. To establish time budgets, individual foragers were tracked from six focal colonies on four different days; we recorded travel distance, travel time, search time, and success for 51 trips (ranging from seven to 10 per colony), of which 44 were used. To establish the spatial distribution of ants, we measured total ants per square meter at 87 sites on 14 d. The sites were centered around the six focal colonies, with 12 sites near the three focal colonies in the crowded region and 16–19 sites near the three focal colonies in the uncrowded region. Speeds, densities, and time budgets were found to be similar to those in other studies of ants in this genus (DeVita 1979; Crist and MacMahon 1991; Haefner and Crist 1994; Morehead and Feener 1998).

We next compare the measured time budgets and ant densities with values predicted by the models. We check whether the models are quantitatively consistent with measured values and assess whether the simpler individual-level model performs better than the more complex colony-level model that includes conflict costs.

Both the colony-level and individual-level models predict search times accurately (fig. 6), with the two models having nearly identical log likelihoods. Measured travel and search times do not show the decrease in search time

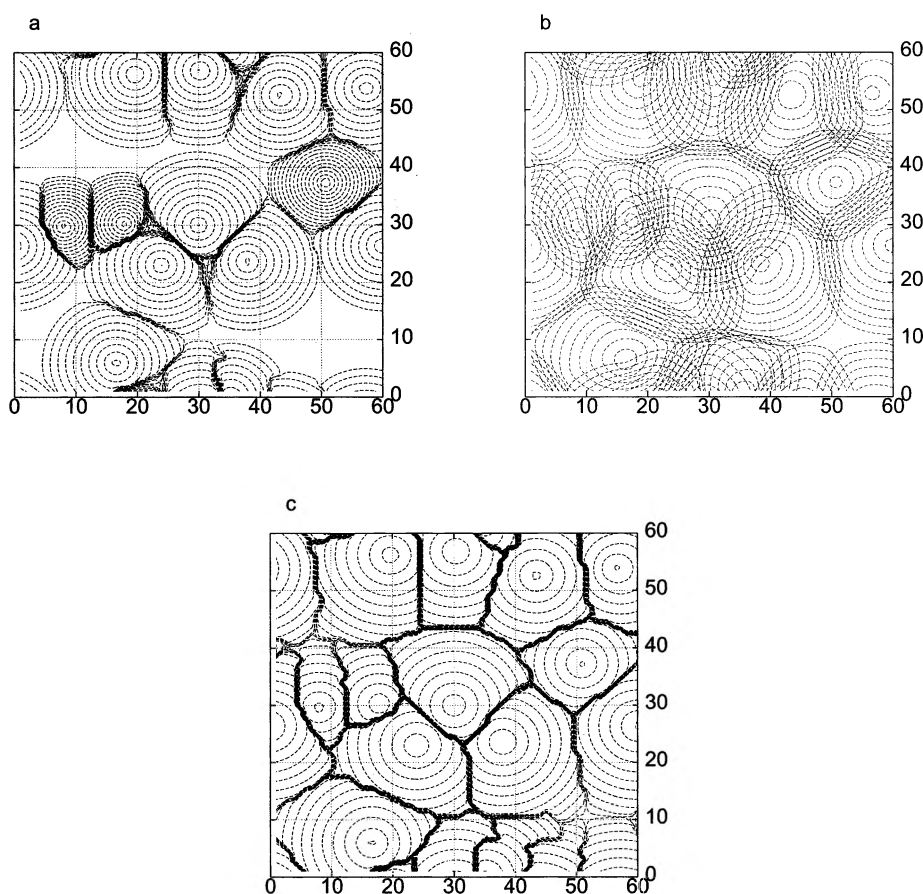


Figure 5: Contours of foraging effort (number of foragers searching) in the crowded region. Contour levels run from 1 to 10 ants/m², and distance is in meters. Parameter values as in table 2 except as noted. *a*, Individual-level strategy. *b*, Colony-level strategy without conflict costs ($\alpha = 0$). *c*, Colony-level strategy with conflict costs.

as a function of travel distance predicted by each model. The colony-level model has a lower slope and qualitatively fits the data better. As a test, we created a modification of the individual-level model in which ants weight search time more heavily than travel time (thus equalizing search times), but this model is not supported by the additional analyses.

The individual-level model accurately predicts the mean distance ants move (fig. 7), while the colony-level model overestimates the mean. Both models predict a lower variance than observed (and are therefore rejected by a Kolmogorov-Smirnov test at the 0.05 level). This deviation may occur because these simplified models ignore movement during the searching process itself, which could spread ants assigned to a given site. Furthermore, ants were tracked in pairs, one that left early in the day and one that left later. Because distances traveled increase during the day, these pairs would tend to include one short and one long foraging trip, leading to increased variance.

Our models are designed to average over these effects, and the individual-level model is thus quite successful in predicting the average.

Finally, each model explains a significant portion of the variance in measured ant density (fig. 8). The colony-level model produces a slope of 0.69, closer to the predicted value of 1.0. Although some of the variance is due to lower densities in the uncrowded site, analysis performed on the two sites separately gives similar results. Stepwise regression indicates that the colony-level model is better supported by the data.

If we tentatively accept the colony-level model, we can examine patterns of deviation between model predictions and measured values. Sites with more ants than predicted tend to lie close to predicted boundaries, while sites with fewer ants than predicted lie farther from boundaries (fig. 9). There is no effect of distance to the nest on the deviations between predicted and measured densities. Results

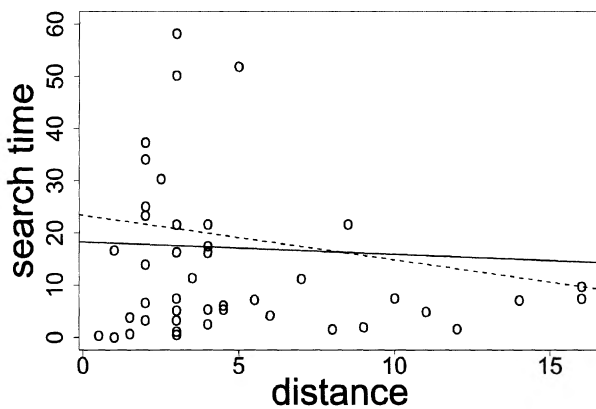


Figure 6: Search time as a function of distance traveled before search begins, comparing data (circles), the colony-level strategy (solid line), and the individual-level strategy (dashed line). Cox proportionate hazards regression shows no effect of distance on search time ($p = .24$), particularly after the effect of time of day is removed ($p = .65$). Including the effect of colony, the colony-level and individual-level models have nearly identical likelihoods (-159.2 and -160.1 , respectively) if search times are assumed to be exponentially distributed.

with the individual-level model are similar, although there is a weak effect of distance to nest.

We tested sensitivity by measuring outputs for a range of parameter values (table 3). The results are highly insensitive to the combined parameters A and K . The spatial distribution of ants is relatively insensitive to the value of b , but search times are sensitive because this parameter determines the standing crop. We chose a value that gave results consistent with the observed travel times. All results are sensitive to the value of σ and affect both foraging ranges and travel times.

Discussion

On the basis of independently measured parameters describing resource dynamics, time budgets, and costs of conflict, we develop relatively simple models of individual behavior that predict the observed low levels of overlap between foraging ranges of neighboring colonies of red harvester ants and quantitatively fit more detailed measurements of ant time budgets and densities. We compare individual-level optimization with more complex colony-level optimization, both with and without incorporation of the time and energetic costs of conflict. The individual-level model, with or without inclusion of conflict costs, predicts realistically low levels of overlap between foraging ranges and provides a reasonable quantitative fit to measured time budgets and densities. The colony-level model that does not include costs of conflict predicts unrealistically high levels of overlap between foraging ranges. The

colony-level model that does include conflict costs predicts realistic patterns of overlap and gives the closest fit of all models to measurements of individual ants and densities.

While we could reject the colony-level model in the absence of conflict costs, we were unable to distinguish the much subtler difference between the individual-level model and the colony-level model that includes conflict costs. Both models predict mean search times and their weak dependence on travel distance equally well (fig. 6). However, only the individual-level model correctly predicts the mean distance traveled by foragers (fig. 7). Both models predict a significant portion of the variance in measured ant densities, but the colony-level model provides a better fit in a multiple regression analysis that includes both models (fig. 8).

These relatively simple models cannot predict every detail of the complex pattern of space use by ants. To understand which missing factors are important, we now consider deviations of model predictions from data and the model generalizations that could address them. We then discuss the missing factors and conclude by describing how this modeling approach could be generalized to other systems.

There are three main deviations of model predictions from the data. First, the effect of distance traveled on search time is weak (fig. 6). This could occur for two reasons: depletion might be unimportant in this system or foraging effort might be sufficiently uniformly distributed in space to equalize the standing crop of resources (Davies and Houston 1981; Possingham 1989; Dreisig 2000; Lewis and Moorcroft 2001). Depletion has been observed in some ant systems (Crist and MacMahon 1992)

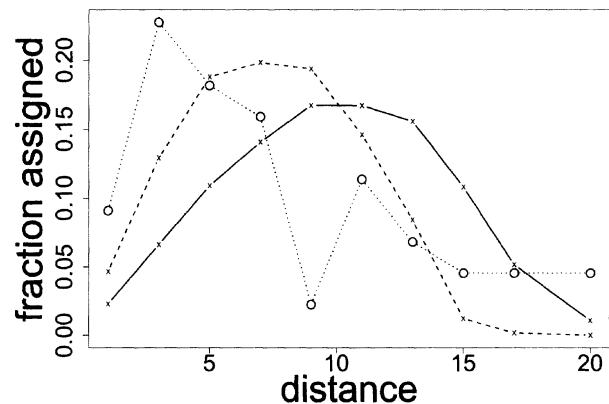


Figure 7: Distribution of distances to discovery of food, comparing the data (dotted line) with the colony-level model (solid line) and the individual-level model (dashed line). Mean distances are 7.5 m for the data, 9.0 m for the colony-level model, and 7.4 m for the individual-level model.

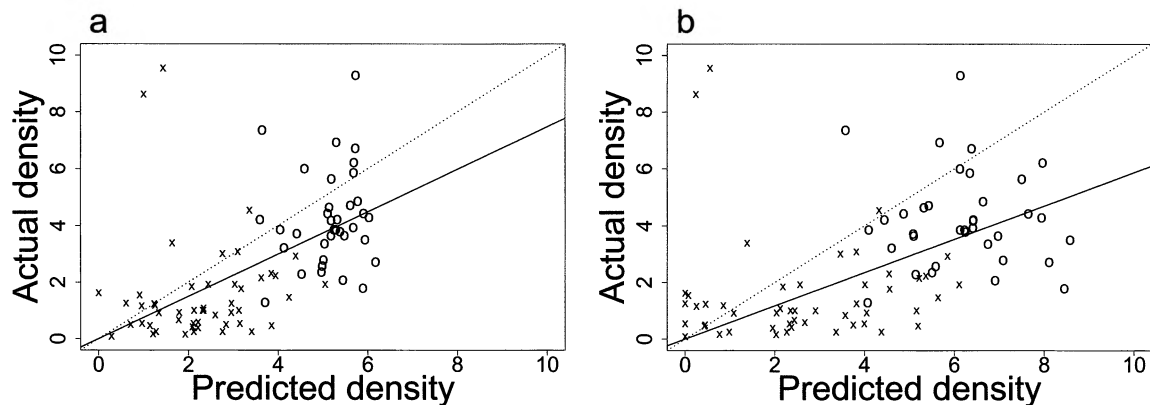


Figure 8: Density of ants in the 87 sites measured plotted against the predictions of (a) the colony-level model and (b) the individual-level model. Circles indicate the crowded region, and crosses indicate the uncrowded region. Density estimates from the model include ants traveling on their way to or from a foraging site, assuming they walk in straight lines at 2.5 m/min. The solid line is the linear regression constrained to pass through the origin, and the dotted line is the diagonal with slope 1. The slopes of the regression lines are 0.69 and 0.58 and the adjusted r^2 values are 0.67 and 0.64 for the colony-level and individual-level models, respectively. Both have $r^2 = 0.65$ and $p < .0001$. When both models are included in a single multiple regression, the individual-level model is removed by stepwise regression.

but not in others (Deslippe and Savolainen 1995). If depletion were unimportant, the observed reduced reproduction of crowded colonies in a dry (resource-poor) year (Gordon and Wagner 1997) would have to be due to interference. Lack of such an effect in a wet (resource-rich) year (Wagner and Gordon 1999) indicates that the importance of depletion varies over time. We thus hypothesize that depletion is in fact significant and that the result is due instead to foraging effort being uniformly distributed in space. Measured densities show only a weak effect of distance from the nearest nest, consistent with the tendency of a colony-level strategy to allocate ants relatively evenly in space (fig. 2).

Second, the distances traveled to find food fail to capture the variance. Although the individual-level model captures the mean distance accurately, it predicts too few ants both near and far from the nest. The colony-level model overestimates the mean (fig. 7). The models simplify foraging by assuming that ants search only in a single site, while in fact ants continue to move while searching (Gordon 1999), spreading searching ants both toward and away from the nest. In addition, ants forage at greater distances during the course of the day, potentially increasing the variance. Finally, using the measured densities, we observe more ants near boundaries than are predicted by the models (fig. 9), perhaps because of vigilance and return to contested sites (Brown and Gordon 2000), marking (Lewis and Moorcroft 2001), other forms of signaling, or defense by depletion (Lucas and Waser 1989), none of which is included in the models.

Third, the models consistently predict higher densities

than are actually observed (fig. 8). This difference might be due to an overestimate of the number of foragers active at any one time but could be a consequence of a low estimate of seed availability.

Our models do not specify the mechanism by which ants achieve a given allocation. Some communication is required (Bartholdi et al. 1993; Pacala et al. 1996; Seeley 1997), which could be indirect through pheromones or direct through contact. Decisions could also include components of individual memory or fidelity (Fewell 1990; Crist and MacMahon 1991; Haefner and Crist 1994; Brown and Gordon 2000). The predictions of the model are independent of the mechanism used, as long as it adjusts to conditions sufficiently quickly. These ants use the rate at which other foragers return as a cue to forage (Gordon 2002), but it is unknown whether they also use more detailed information about search times, distances, or directions. Although it is not clear how ants might communicate all the information required to achieve an optimal distribution that includes conflict costs, complex optimal strategies can be approximated with relatively simple rules (Pacala et al. 1996). A model of interactions between wolf packs predicts a spatially uniform density of prey without any communication between members of the same pack (Lewis and Moorcroft 2001). Spatial distributions in this model are entirely enforced by avoidance of the scent marks of the other pack.

The models also neglect many forms of heterogeneity. Our predictions average over an entire foraging season (Gordon 1999), over different seed types (Ferster and Traniello 1995; Detrain et al. 2000), over foragers that

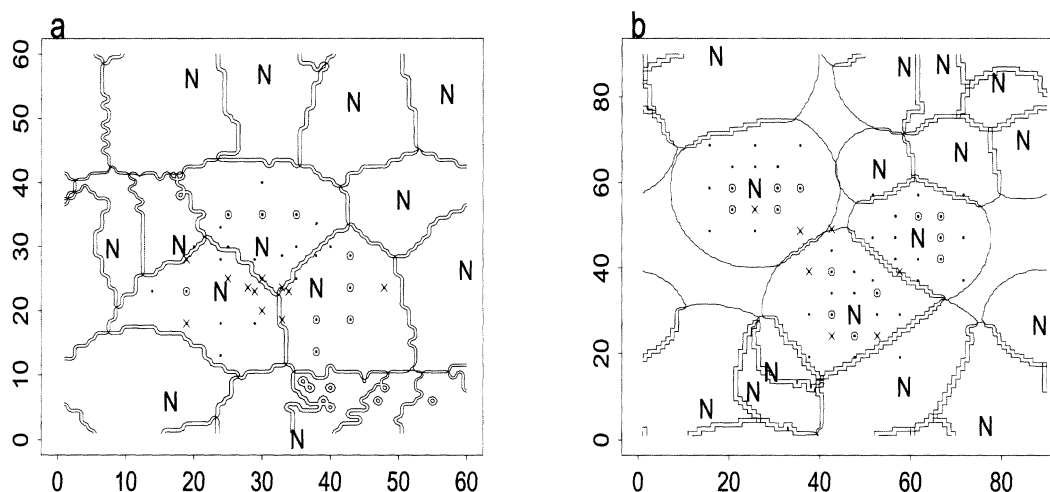


Figure 9: Patterns of deviation from densities predicted by the colony-level model in (a) the crowded region and (b) the uncrowded region. The *N*'s indicate colony locations, and the contours indicate the outer boundary of the foraging range. Crosses show sites where predictions (on the basis of the linear regression in fig. 8b) are low by more than 1.0 ants/m², circles show sites where predictions are high by more than 1.0 ants/m², and dots show sites where predictions are within these bounds. Multiple regression indicates that the effect of distance to the boundary is significant ($p = .02$), while there is no detected effect of distance to the nearest nest.

might show some degree of specialization (Brown and Gordon 1997), and over spatial heterogeneity (Davidson 1977). In the absence of sufficient data, we have not evaluated whether these factors have a large effect on the long-term payoffs evaluated in our models. However, as argued in the derivation of the models, two aspects of the resource dynamics imply that space use will average out over the course of a foraging season. First, seed distributions are unpredictable and temporally variable, meaning that all sites might be equally valuable on average. Second, the dynamics of seed removal are sufficiently slow that any resource pulse need not be removed immediately as long as a particular colony has access to that site.

Species in the genus *Pogonomyrmex* live in a variety of habitats, from grassland to desert, so their foraging environments vary in resource type and distribution. Comparative studies show that species differences in mor-

phology and in physiological response to temperature lead to differences in seed selection and the energetic costs of foraging (Fewell 1988; Ferster and Traniello 1995; Weier and Feener 1995; Morehead and Feener 1998). The genus shows diversity in the spatial patterns of a colony's foraging trails (more established trunk trails in *Pogonomyrmex occidentalis* [Crist and MacMahon 1992] than *Pogonomyrmex barbatus* [Gordon 1992]), in the directional and patch fidelity of individual foragers (higher in *P. occidentalis* [Fewell 1990] than other species [Holder Bailey and Polis 1987; Crist and MacMahon 1991; Crist and Haefner 1994; Haefner and Crist 1994]), in the intensity of intraspecific aggression (higher in *Pogonomyrmex californicus* [DeVita 1979] than *P. barbatus* [Brown and Gordon 1997]), and in the spacing of populations (Davidson 1977; Wiernasz and Cole 1995; Gordon and Kulig 1996). The other well-studied genus of seed-eating ant is *Messor*, in which species also differ in foraging behavior and intraspecific interactions (Acosta et al. 1995; Yamaguchi 1995; Brown and Gordon 2000). It is difficult to know to what extent different species would respond in the same way if they encountered the same conditions. When we can explain in detail the diverse behavior of several species, it may be possible to generalize about the evolution of the foraging behavior of harvester ants.

Although these models were developed for a particular species and population, the methods should be applicable to other ants, bees, and modular organisms such as plants (Silvertown and Gordon 1989; Lopez et al. 1994). Different organisms or groups might differ in their degree of phys-

Table 3: Sensitivity to parameters

Parameter	Range of values	Mean distance ^a	Mean travel time ^b	Regression slope ^c
σ	.05–.2	6.11–8.49	8.57–30.26	.57–.72
b	.5–2.0	7.39–7.41	10.51–26.20	.66–.79
A	.015–.06	No effect ^d	No effect	No effect
K	.01–.04	No effect	No effect	No effect

^a The predicted average trip distance using the individual-level strategy.

^b The predicted average trip time using the individual-level strategy.

^c Slope of the regression of actual versus predicted numbers using the individual-level strategy.

^d Results unchanged to two decimal places.

iological integration and ability to transfer and use information and in the balance between common interest and conflict of interest. We would not expect unrelated individuals in a group foraging species to allocate themselves in space according to the colony-level model. Ecologically, key distinctions among species might result from resource dynamics (e.g., the water sought by plants has much faster dynamics than the seeds collected by harvester ants), the flexibility of foraging strategies, and the costs and benefits of conflict. By building on measurements of individuals, these models have the potential to make sense of the extent and type of conflict in a wide range of species with local resource competition.

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